XVI. *The structure and life-history of the Holly-fly.* By Professor L. C. Miall, F.R.S., and T. H. Taylor.

[Read March 20th, 1907.]

I. Introduction.

Occurrence.—Holly-leaves are often infested by a small Dipterous larva, which forms discoloured blisters upon them. When opened with a needle the blisters are found to contain yellowish-white larvæ with black heads and tails. In particular localities a large proportion of the leaves may be disfigured in this way, and it was the abundance of the insect near Leeds which caused us to undertake its investigation.

Goureau * has published a slight notice of the holly-fly, to which he gave the name of *Phytomyza aquifolii.* We have not attended to the classification of Phytomyza, and express no opinion upon the validity of the species.†

Summary of Life-history.—The life of the holly-fly occupies about a year, and extends from one June to the next. In June the young leaves of the tree are expanding, and the eggs are laid in the midrib while it is still tender. The larva soon hatches out, and remains in the midrib for about two months, boring its way along the central vessel (fig. 1). Then it turns aside, and enters the blade of the leaf, feeding on the green cells beneath the upper epidermis, and producing a blister of irregular shape, which at first takes a pale colour in consequence of the contained air. More than one larva may attack the same leaf, and their blisters sometimes run together. The cuticle is too opaque for the larva to show through it, but it can be felt by gentle pressure with the finger-tip. When feeding it lies on either its right or left side, and mows down the cells with its mouth-hooks, leaving a track which, while fresh, is visible from without, and reminds one of the path made

* Ann. Soc. Ent. France, vol. ii, p. 143 (1851).

† There is a brief notice of the holly-fly in Réaumur's "Histoire des Insectes," vol. iii, mém. 1 (1737).

by the radula of a pond-snail among the microscopic algæ of an aquarium. About the end of March the larva is full fed, and turns to a pupa, which, unlike that of many other leaf-miners, remains within the leaf. The flies appear about the end of May, and may be seen throughout

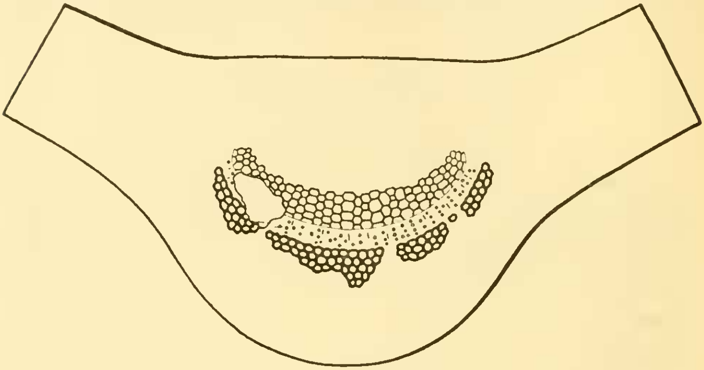

Fig. 1.

Transverse section of midrib of holly-leaf showing larval mine in central vein. (× 50.)

June on infected holly-trees, usually alighting on the young green shoots. We have not met with them except on the holly, nor have we seen them fly except from one leaf to another.

II. The Structure of the Larva.

We shall begin by describing the larva in its first stage, and then notice the points of difference which mark the full-grown larva.

The Exoskeleton. The body (fig. 2) consists of a head succeeded by three thoracic and nine abdominal segments, the two last of which are distinguished with difficulty.* Transverse bands of minute hooks make the junctions of the segments obvious, except where the 11th and 12th segments meet. The first band is restricted to the dorsal surface; the second is interrupted laterally; all the bands are interrupted along the mid-dorsal and mid-ventral lines.

* Twelve is the usual number of post-cephalic segments in Muscid and Nemoceran larvæ. In one species of Chironomus we have found faint indications of a subdivision of the 12th larval segment, the part behind the bunches of setæ being constricted off.

The head is sunk into the thorax so deeply that only

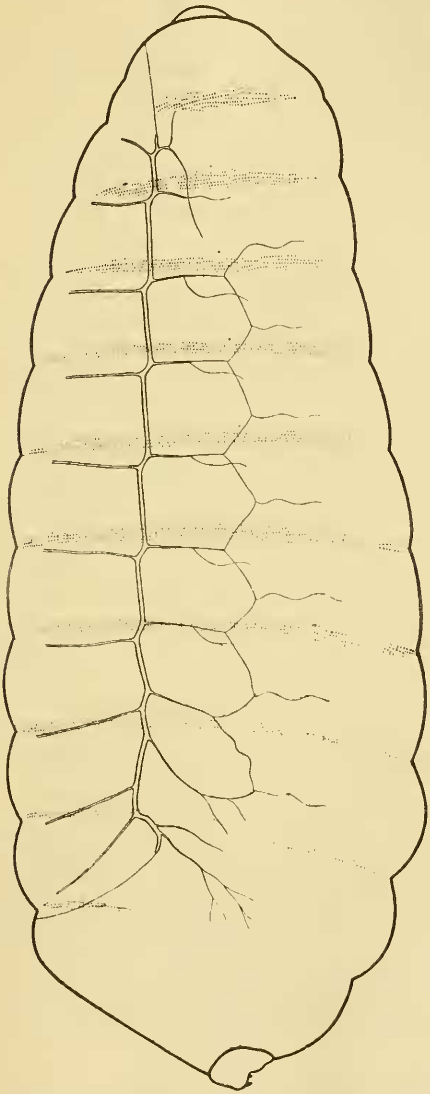

Fig. 2.

Larva of first stage, lateral view, showing external features and tracheal system. The longitudinal tracheal trunk terminates anteriorly and posteriorly in an initial thread which is connected with a closed spiracle; the dorsal commissures are continuous with those of the other side. (× 145.)

the extreme fore-end is exposed. It is long and narrow, and reaches as far back as the metathorax. The ventral

surface of the exposed part is strongly chitinised, and serves for the prehension of food. In the young larva it is armed with three hook-like teeth, one median and of larger size, the other two smaller and further back. This chitinised ventral plate, which, although it is deeply cleft behind, is apparently single, is replaced in older larvæ by two unequal oral plates, enclosing the mouth-opening between them, and each carrying two hook-like projections. Muscles pass from the body-wall to the oral plate or plates, and effect the movements necessary to mastication. In young larvæ, but not in older ones, a pair of curved chitinous struts, standing off on either side at right angles, probably serve to hold the plate in position (they are omitted from fig. 3). The upper-surface of the head is almost entirely concealed; on the minute exposed part are several small oblique sunk rods of chitin, of unknown function. The head-capsule, which answers to the wall of the head in more normal insects, consists of a delicate cuticle, lined by an epidermis. It is continuous with the oral plates, but otherwise completely immersed; nothing can be seen of an invagination-cavity. Muscles pass from the body-wall to the head-capsule. There is also an endocranium, which we suppose to have originated in chitinous apodemes; it consists of an anterior median piece, deeply grooved on its upper-surface, and a posterior forked piece, divided into right and left halves, each of which gives off dorsal and ventral arms. The groove on the median piece lodges the pharynx.

The Nervous System.—The central nervous system (fig. 3) is lodged in the thorax and the fore-part of the abdomen; it consists of cerebral ganglia and a ventral complex. From the latter paired nerves are given off to the head (three pairs), to all the thoracic segments, and to the first eight abdominal segments. A pair of large ganglia in front of the cerebral ganglia may represent the optic lobes of the blow-fly larva. The prothoracic and mesothoracic nerves have ganglia at their roots. No sense-organs have been clearly made out in the young larva, though in older larvæ minute structures, which are probably sensory, appear on the exposed surface of the head (fig. 5).

The Alimentary Canal.—The mouth-opening leads into a small buccal cavity, which lies within the oral plate. The fore-part of the pharynx is strongly chitinised, and

connects the oral plate with the endocranium; the hinder-

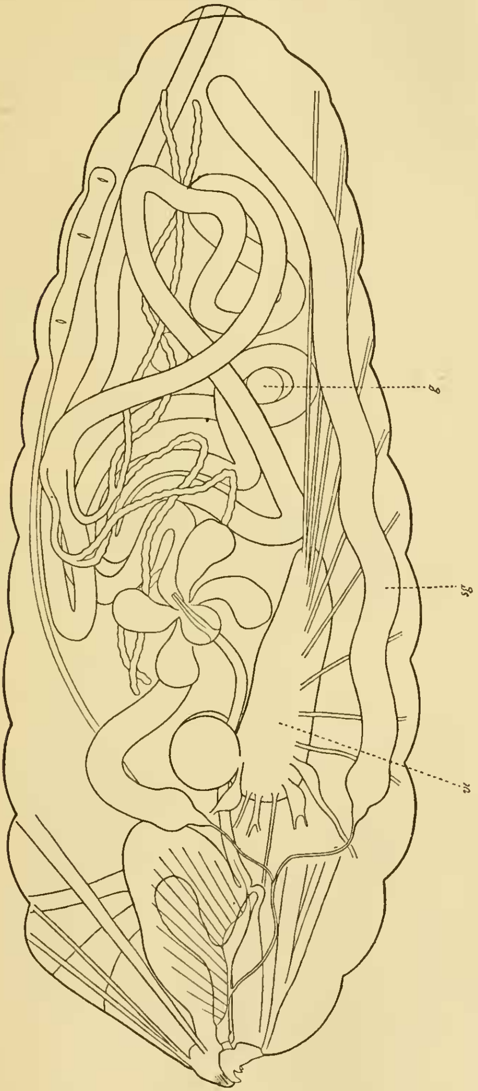

Fig. 3.

Larva of first stage, showing internal anatomy. *g*, gonad; *sg*, left salivary gland (the anterior end only of the right gland is shown); *vc*, ventral complex of nervous system. (× 145.)

part lies in the concave median piece of the endocranium, and behind this in the space between the diverging

ventral arms. A series of muscles, which are inserted into the dorsal wall of the pharynx, probably serve to dilate the cavity; when a live larva is placed in water charged with finely-powdered carmine the particles can be seen to enter the mouth at each contraction of the muscles. The œsophagus (fig. 3) passes between the cerebral ganglia. There is a cardiac chamber, with four cæca and an œsophageal valve. The stomach is long and convoluted. Two Malpighian tubules, each bifurcate, enter the beginning of the intestine. The whole alimentary canal is about five or six times as long as the body. The salivary-glands reach to the hinder-end of the body; they are slightly dilated in front. Their ducts unite into a single tube, which opens into the floor of the pharynx, perforating the median piece of the endocranium in order to do so; they show the usual cross-marking. It is hard to explain the large size of the salivary-glands, but as no pupal cocoon has to be made, their function is probably strictly alimentary.

The Tracheal System.—A pair of longitudinal tracheal trunks run nearly the whole length of the larva (fig. 2). These trunks are connected with each other by transverse dorsal commissures, and give off segmental branches. Adjacent segmental branches are united by longitudinal connectives, from each of which arises a ventral trachea. There are ten pairs of closed spiracles, two thoracic and eight abdominal. The first and the last pairs occur respectively in the 1st thoracic and the 8th (spiracular) abdominal segment, and are placed near the mid-dorsal line; the remaining spiracles are lateral in position, each being placed close behind one of the bands of segmental hooks. The anterior and posterior spiracles are often unusually large in Dipterous larvæ; in the holly-fly they are closed like the rest in the young larva, but become functional in the later larval stages. The tracheal junctions which divide the longitudinal trunks into segmental systems are evident in the last larval stage.

The Dorsal Vessel.—The dorsal vessel or heart (fig. 3) is three-chambered, each chamber being provided with a pair of ostia. The fore-end of the dorsal vessel reaches the head-capsule and is attached to it, but actually opens into the thorax.

The Fat-body.—Between the coiled strings of the fat-body are found bright refractive bodies of large size (fig. 4),

which are calcareous concretions, each enclosed within a nucleated cell. They present a rough surface, and an internal concentric lamination resembling that of a starch-grain. Similar concretions are found in the proglottides of a tape-worm.

The fate of the concretions of the holly-fly larva is interesting. They persist throughout the larval stage, gradually increasing in size, but disappear soon after pupation. In an old puparium the internal tissues are devoid of lime-salts, but the cuticle effervesces strongly as soon as its inner surface is touched with acid. It seems likely that the substance of the concretions is absorbed and re-deposited in the cuticle.* Occasionally a few concretions persist and are carried over into the fly.

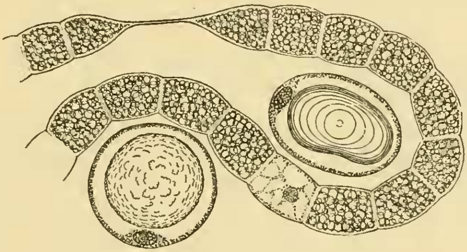

FIG. 4.

Cells of the fat-body. Two calcareous corpuscles are shown, one in surface-view, the other in optical section; the fat-globules have been omitted from one cell. (× 625.)

The Gonads.—Two spherical bodies (fig. 3) lying between the coils of the intestine are the gonads; they remain practically unchanged throughout the larval period.

Larval Stages.—The larva of the holly-fly moults twice before pupation; there are thus three larval stages. The first lasts from July to December; the second from December to February, and the third from February to the middle or end of March. At times of moult the skin splits along the *ventral* side, which is unusual in insects. At pupation the larva is 3·5–4 mm. long.

The peculiar features of later Larvæ.—A larva of the second or third stage differs from the larva which has just

* A similar transference probably occurs in other Dipterous leaf-miners, *e.g.* in *Acidia heraclei.*

been described in several particulars. There are now two oral plates, one on either side of the mouth-opening, the right plate being larger than the left. Each bears two hooks, which are probably used in dividing the food. The anterior hook of the right plate is the largest of the four, and the distortion which regularly occurs brings it exactly in front of the mouth-opening (fig. 5). The asymmetry of the oral plates may be connected with the circumstance

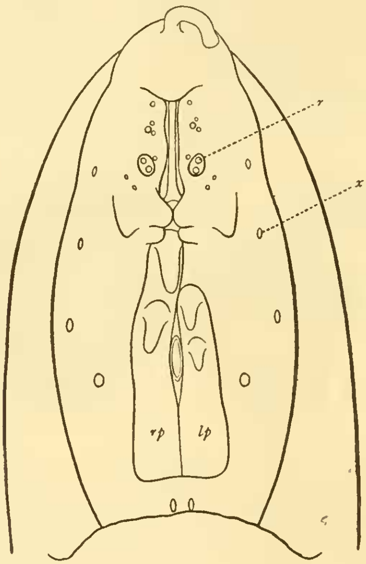

FIG. 5.

Head and prothorax of larva of 3rd stage, ventral view. *lp*, *rp*, left and right oral plates; *r*, oblique sunk rods; *x*, chitinous rings. (× 360.)

that the larva lies on its side while feeding on the cells of the leaf. The endocranium is stronger and of darker colour, almost black. The anterior median piece has become distinct from the forked part (fig. 6). A new structure, the tentacle, now appears on the exposed surface of the head; what seems to be the labrum is produced into two pairs of lobes; there are also for the first time chitinous rings on the head and prothorax which resemble the bases of setæ and are perhaps sensory (no true setæ have been seen on any part of the cuticle); the oblique sunk rods are more conspicuous. The segmental bands of

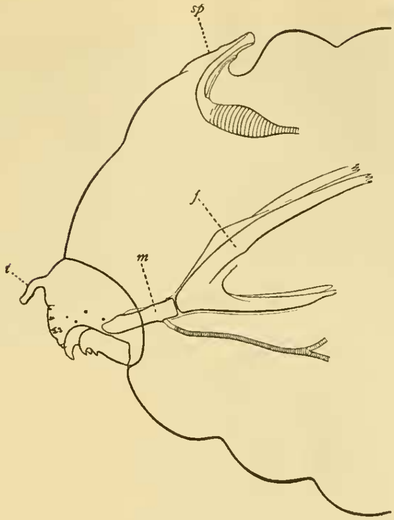

FIG. 6.

Head and thorax of larva of 3rd stage, lateral view. *f*, forked plate of endocranium; *m*, median ditto; *sp*, anterior spiracle; *t*, tentacle. (× 200.)

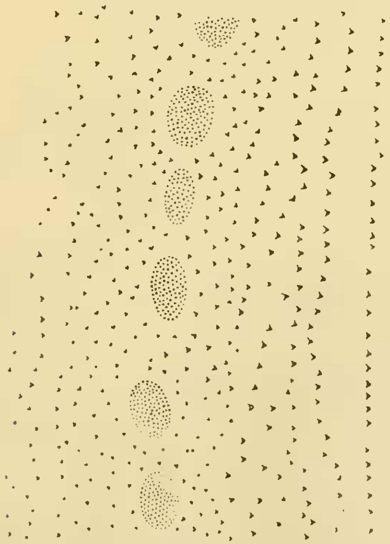

FIG. 7.

Portion of segmental band of hooks from larva of 3rd stage, showing the muscular insertions (dotted); the hooks point backwards. (× 430.)

hooks become broader and the hooks more numerous. Areolæ, devoid of hooks, and answering to the attachments of segmental muscles, are found in the bands (fig. 7). In the third stage the 3rd–6th bands are continuous dorsally. The tracheal network is richer, and the anterior and posterior spiracles are functional, their initial threads having been replaced by open extensions of the main trunks (tracheal extensions).

The spiracles have already been described as they appear in the first larval stage. We go on to describe the spiracles of the last larval stage, and then notice those of

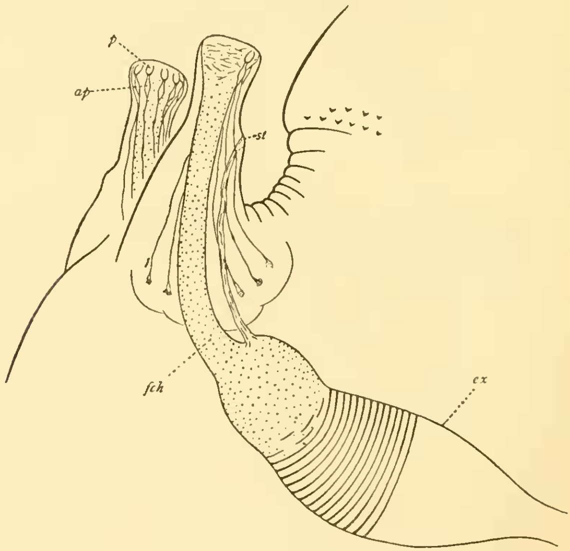

Fig. 8.

Anterior spiracles of larva of 3rd stage. *ap*, earring-like appendage with filament; *ex*, tracheal extension; *fch*, "felted chamber"; *p*, pit; *st*, closed spiracle with cord ("Narbenstrang"). (× 280.)

the second larval stage, which are intermediate in structure between the earlier and later ones.

In the third stage the anterior and posterior spiracles project from the surface of the body. The anterior spiracle (fig. 8) is a compound structure ("compound spiracle" of De Meijere*) consisting of a functional and a closed spiracle, both carried on a cuticular process of the skin. The internal part of the functional spiracle

* Zool. Jahrb., vol. xv, pt. iv, p. 623 (1902).

consists of an air-containing cylinder ("felted chamber") which, arising from the end of the tracheal extension, runs up the stalk and terminates in an expanded "end-plate." The closed spiracle is attached to the side-wall of the stalk and connected by a solid cord ("Narbenstrang") with the end of the tracheal extension. The cavity of the air-containing cylinder is subdivided by chitinous trabeculæ into minute spaces, and presents a dotted appearance when the air has been removed by alcohol. The end of the tracheal extension has the same structure. The end-plate of the spiracle is flattened from side to side, and carries on its inner and posterior faces six or more radiating pits (the number is not constant). Each pit has a thickened

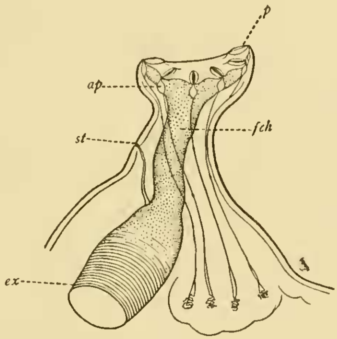

FIG. 9.
Posterior spiracle of larva of 3rd stage.
Lettering as in fig. 8. (× 330.)

margin from which an oval appendage hangs down like an earring in the space outside the air-containing cylinder. From each appendage a delicate filament is given off, which, passing down the stalk, branches and ends in intricate beaded coils, resembling the termination of a nerve on a muscle-fibre. The structure of the posterior spiracles (fig. 9) is similar to that of the anterior ones, the felted chamber, pits, appendages and filaments, and the closed spiracle being all present. The pits are more elaborate, and resemble miniature spiracles; they are carried on prominences which are situated on the outer side of the end-plate, and vary in number from five to nine, the number being usually different in the two spiracles. Each pit apparently opens to the exterior by a slit.

In the second larval stage the tracheal extensions are not dilated, but each is connected with an air-containing cylinder terminating in an end-plate, which forms a knob-like projection on the surface of the body. The pits with their appendages and filaments, if they are actually present, are difficult to demonstrate.

III. Pupation.

About the middle of March the larva is full grown and ready for pupation. It is still imprisoned within the leaf, but can move freely about in the blister, which is now a large open space lying between the leaf-veins and the epidermis. The palisade-cells are always the first to be attacked; sometimes the spongy cells are excavated as well, but this comes later; in any case the epidermis with the cuticle is left intact.

Before pupation the larva prepares an opening, through which it may afterwards emerge as a fly. To this end it pares down the epidermis in one place until only the external cuticle remains. This area, which may be called the "pupal blister," is parabolic in plan, and although very small is easily distinguished from the rest of the larval blister by its different colour. The apex of the pupal blister is sharply defined, but the base gradually shades off. It now becomes possible to observe the movements of the larva through the transparent cuticle. The edge of the pupal blister is pierced; the larva turns over and lies on its back with the ventral surface pressing against the cuticle; the movements of the oral plates become slower and at length cease. Two short black rods now become visible in a strong light; these are the anterior spiracles projecting from the top of the prothorax. At first they lay behind the exposed part of the head, and pointed upwards and backwards. The head is now completely retracted into the thorax, and the spiracles occupy the front extremity of the body, having swung round so as to point forwards. After a few preliminary trials they are passed through the slit in the cuticle, and become fully exposed to the outer air. They form a black speck on the apex of the pupal blister, and can easily be felt by the finger-tip.

IV. The Pupa and the Emergence of the Fly.

The pupa, shrouded in a delicate transparent membrane

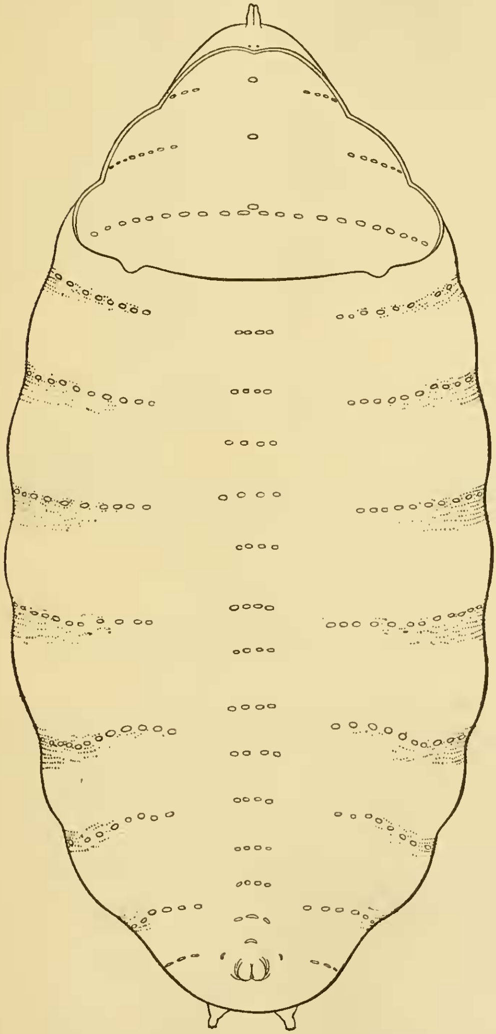

Fig. 10.

Puparium, ventral view. The hinged plate has been removed; the hooks and insertions of larval muscles are shown. (× 45.)

(the true pupal skin), remains enclosed in the larval cuticle, which has become much thickened by calcareous deposit

on its inner surface. By appropriate methods the thin larval cuticle can be separated from the later calcareous addition. The body of the puparium (fig. 10) is rusty in colour, with a smooth shining surface, and flattened dorso-ventrally. The larval head has been completely retracted, and the fore-part of the prothorax, sharing in the movement of retraction, forms a funnel-shaped depression on the front part of the ventral surface of the puparium. This depression is partly filled up with a waxy secretion, which appears at the mouth just before the movements of the larva cease. The spiracles, anterior and posterior, are now black and strongly chitinised. The fly escapes from the puparium by a hinged plate (fig. 11) which very nearly coincides in position and extent with that special part of the general blister which we have called the

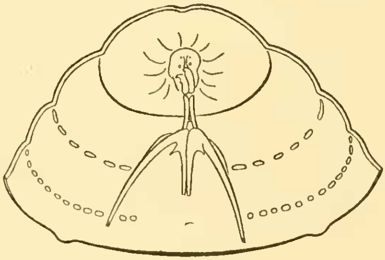

Fig. 11.

Hinged plate of puparium. The oral and endocranial plates of the larva remain attached to the inner surface. (× 45.)

"pupal blister." When the fly is ready to emerge the plate is raised in front and pushed back (fig. 12), bringing with it the cuticle of the blister. The rupture is effected by the alternate swelling and contraction of the frontal sac of the fly, which is very distensible and roughened on the outer surface with numerous fine denticles. The ventral surface of the fly appears first with the legs. The wings are crumpled when they are withdrawn from their sheaths, but soon expand.

Empty pupal cases in blistered holly-leaves can easily be identified by the raised hinged plate. Sometimes, instead of the raised plate, one finds in the pupal blister a small circular aperture; this marks the place through which a parasitic ichneumon has escaped, and it is interesting to notice that the ichneumon quits the puparium and

leaf at the place of weakness which has been made ready for the escape of the fly. We have not attended to the ichneumon parasites of the holly-fly further than to note that there are two distinct species at least, one appearing early in June and the other later in the summer. We have found parasitic larvæ in holly-fly larvæ of all ages, but are unable to say when or how the eggs are deposited.

Cyclorrhaphous and Orthorrhaphous Diptera.—The larval skin, which forms the wall of the puparium, is marked by prepared lines, which facilitate the escape of the fly. In the holly-fly one line begins on the prothorax, just below the spiracle, passes horizontally back to the fore-part of

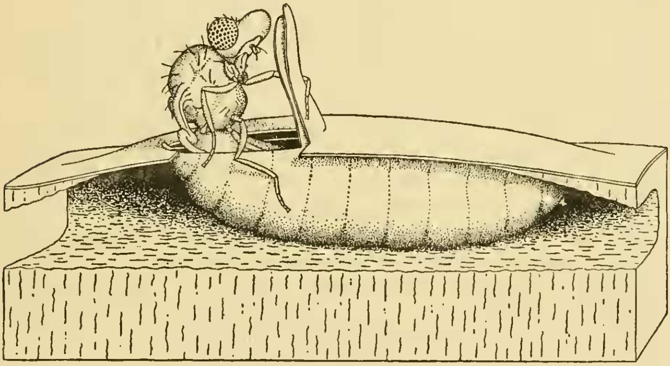

FIG. 12.

Fly emerging from puparium. (× 20.)

the 1st abdominal segment, and there forks into a descending and a slighter ascending branch. It will be convenient to speak of these lines as "lines of dehiscence." * In the holly-fly the horizontal line of dehiscence, together with the descending one, marks out a triangular ventral plate, which can be turned back as on a hinge to allow the fly to escape. In Drosophila a similar horizontal line of dehiscence runs along the thorax, and then forks as in the holly-fly. Here, however, the ascending branch is the

* Such lines have been called "sutures," a term which is open to objection, because it suggests the line of union of distinct morphological elements, as in the phrase "sutures of the skull." They differ, on the other hand, from lines of fracture in being prepared in advance; they can be traced in a puparium from which no fly has emerged.

stronger and meets its fellow in the mid-dorsal line; the hinged plate is dorsal in position, and the descending branch does not aid in emergence. In the blow-fly the ascending and descending lines of dehiscence practically disappear, being represented by two minute diverging branches at the posterior end of the horizontal line. When the fly emerges the dorsal and ventral halves of the puparial thorax are pushed asunder, and a transverse rupture occurs on the dorsal or on the ventral half, sometimes on both. Thus in the blow-fly the whole thorax often becomes completely detached from the puparium. In Oscinis frit the horizontal line of dehiscence forks into two branches, of which the ascending one, passing about half-way to the mid-dorsal region, is the stronger. At emergence the puparium splits open along the horizontal line, generally along the ascending branch and sometimes also along the descending one.

In all these cases the horizontal line of dehiscence is constant and functional, while the transverse line may be slightly developed and functionally unimportant. It is not at all certain whether Brauer used the term "cyclorrhaphous" of the vertical or of the horizontal line of dehiscence, or of both. In some text-books the writers, evidently basing their statements on what they suppose Brauer to have meant, explain the term "cyclorrhaphous" with reference to what we have called the ascending and descending lines of dehiscence, making no mention of the horizontal one.

The term "orthorrhaphous" is also at present ambiguous. It was originally used by Brauer * to describe a particular mode of dehiscence of the last *larval* skin at pupation. In his later account † he modified his views, and it is not clear to us how his later definition is to be understood, and whether the orthorrhaphous dehiscence is a dehiscence of the larval integument, or of the pupal integument, or of both, or sometimes of one and sometimes of the other. It seems to us that further investigation is called for. Dipterologists may fairly be expected to say with some precision what they mean by the terms "orthorrhaphous" and "cyclorrhaphous," and to indicate the types which they have actually examined.

* Monogr. der Oestriden, p. 33 (1863).
† Zweiflügler des kais, Museums, i, p. 7 (1880).

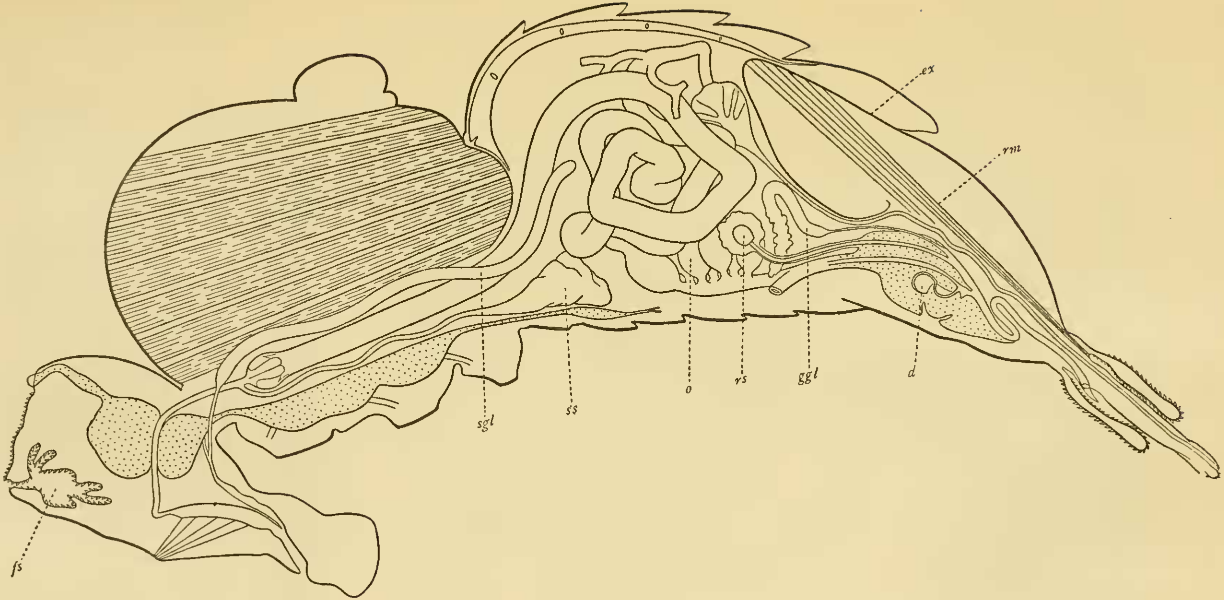

Fig. 13.

Sagittal section of female fly. The Malpighian tubules are cut short. *d*, ventral diverticulum of uterus surrounded by muscular mass; *ex*, conical extension of 7th segment; *fs*, frontal sac (retracted); *ggl*, gluten-gland (only one is shown); *o*, right ovary (the left is not shown); *rm*, retractor-muscles of ovipositor; *rs*, sperm-receptacle (only one is shown : *sgl*, left salivary gland. (× 50.)

V. The Fly.

External Features and Segments.—The mature insect is about 2½ mm. long, the females being rather larger than the males. The body is black in colour. When the abdomen is distended the successive tergal and sternal plates are separated by pale-coloured intervals, and there is also a similar lateral band on each side. The halteres are white.* The abdomen of the female fly consists of nine segments. The 1st is seen with difficulty on the dorsal side, and is represented ventrally by a small plate.

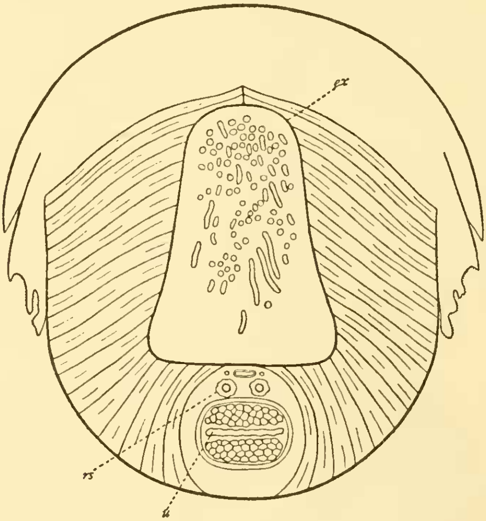

Fig. 14.

Transverse section through 7th segment. *ex*, conical extension, containing retractor muscles of ovipositor, and giving attachment to the oblique muscles of the segment; *rs*, ducts of sperm-receptacles, dorsal to which are the rectum and the ducts of the gluten-glands. (× 115.)

The next five segments are distinctly visible both on the upper and under-surface. The 7th segment differs from the rest in having the sternum and tergum united to form a short tube, into which the ovipositor can be retracted. The upper-front border of this tube is drawn out into a chitinous sheet, which extends throughout the segment next in front; its sides are bent downwards and

* The rest of the description relates to the female fly only.

backwards, so that it forms an inner conical chamber

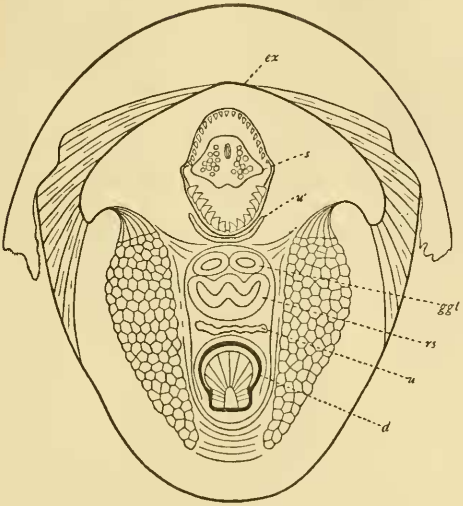

FIG. 15.

Transverse section through 7th segment; the plane of this section is posterior to that of fig. 14. *d*, ventral diverticulum of uterus; *ex*, conical extension of 7th segment, containing 8th and 9th segments (retracted), giving attachment laterally to the oblique muscles, and ventrally to the muscular tissue surrounding the uterus; *ggl*, ducts of gluten-glands; *rs*, fused ducts of sperm-receptacles; *s*, 9th segment enclosed in 8th; *u*, uterus; *u'*, thin-walled region of uterus. (× 140.)

enclosed by the 6th segment (fig. 13). From the wall of this chamber and from its inner surface spring the

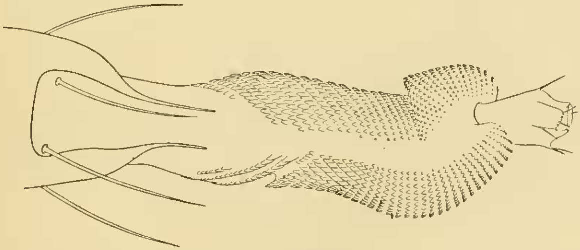

FIG. 16.

Ovipositor of fly, lateral view. The 9th segment is partly retracted into the dentigerous 8th segment; the posterior end of the 7th segment is shown. (× 120.)

retractor-muscles of the ovipositor, while to the outer lateral surface is attached a set of oblique muscles (figs.

14, 15) which pass to the inner face of the tube (7th segment). They enclose between them a median portion of the hæmocœle, in which lies the special muscular portion of the uterus. It is difficult to say whether these oblique muscles effect a change in the shape of the external wall of the 7th segment or in that of the conical extension. It is possible that they serve to protrude the ovipositor by setting up an increased blood-pressure in the last segments of the body. The 8th and 9th segments are specially modified to form the ovipositor. The dorsal and ventral surfaces of the 8th segment bear an elaborate arrangement of denticles (figs. 16, 17) which facilitate the operation of boring into the tissues of the holly-leaf during feeding and oviposition. The 9th and last segment bears at its posterior extremity a pair of short valves. The thin intersegmental cuticle between the 8th and 9th segments is much enlarged, and permits the 9th segment to be completely telescoped into the 8th (figs. 18, 19).

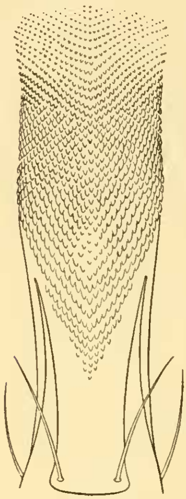

FIG. 17.

Ovipositor of fly, dorsal view. The 9th segment is completely retracted and not shown. (× 120.)

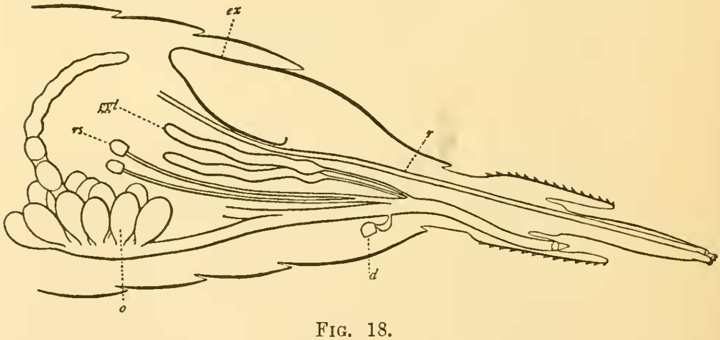

FIG. 18.

Posterior abdominal segments of female fly, diagrammatic. The ovipositor is extended. The left ovary alone is shown; one tubule is complete; *r*, rectum; the rest of the lettering as in fig. 13.

The hinder-part of the 8th can be folded back into the fore-part. When fully retracted, the ovipositor is enclosed

within the tube-like 7th segment. The muscles effecting this retraction arise from the inner surface of the chitinous extension of the 7th segment, and are inserted into the 9th segment, some at its beginning and some further back.

Alimentary Canal.—The general arrangement is similar to that of the larva. The salivary glands (fig. 13) persist, but are much reduced in size. The posterior part of the œsophagus gives off a median ventral diverticulum. This passes back through the thorax as a narrow tube lying below the stomach, and dilates in the abdomen into a very distensible thin-walled sac, which corresponds to the sucking-stomach of other insects. As the pharyngeal

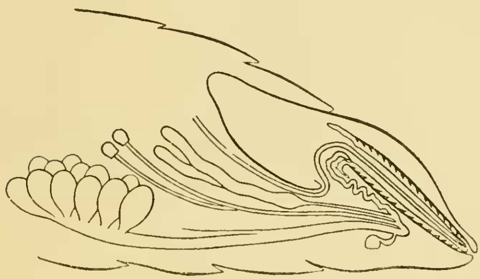

Fig. 19.

Posterior abdominal segments of female fly, diagrammatic. The ovipositor is retracted into the 7th segment.

pump no doubt serves to draw fluids into the mouth, it is rather uncertain what is the special function of the sucking-stomach. The rectum dilates near its beginning into a pyriform chamber, the wall of which is provided with four papillæ.

The Heart.—The heart (fig. 13) lies in the dorsal part of the abdomen. It is widest in front, where it abuts upon the posterior surface of the mesothoracic wall. From its anterior end a fine tube passes downwards and enters the thorax, lying along the dorsal surface of the stomach (this thoracic portion is not represented in fig. 13). Ostia occur in the first five abdominal segments.

The Ovary.—The paired ovary (fig. 13) consists of twelve to fourteen tubules, which are connected at their base with the oviduct. The two oviducts unite to form the uterus, which opens ventrally between the 8th and 9th

segments. A pair of scoop-like plates, situated one on either side of the external aperture, perhaps serve to direct the egg as it emerges from the uterus. The uterus receives on its dorsal aspect the ducts of the receptacula seminis and of the gluten-glands. Both these organs are paired, and the ducts are lined by a chitinous intima which in the case of the ducts of the gluten-glands is spirally wound. Where they join the uterus the muscular wall of the latter is considerably thickened both dorsally and ventrally, giving rise to a conspicuous body of tissue lying in the 7th segment. Imbedded in the ventral portion of this muscular tissue occurs an unpaired hemispherical sac (*d*, figs. 13, 15, 18), which communicates by a short duct with the cavity of the uterus. The walls of both the sac and the duct are strongly chitinous. The floor of the sac as seen in sections strongly arches into the cavity, but as it is provided with muscles it can probably also be depressed; we are unable to explain the function of this organ. Behind this special muscular region the uterus is thin-walled and much elongated to permit of the extension of the ovipositor.

VI. Egg-laying and Eggs.

The eggs of the holly-fly are laid in June. At this time the young leaves are being put forth, while those of the past season are turning yellow. Some six or eight leaves are borne on each young shoot; the lower ones are the first to mature, and for about three weeks there is a constant succession of leaves fit for the operation of egg-laying.

On examining holly-leaves at almost any time of the year a number of pits will often be remarked on both the upper and the lower surface. These first appear when the leaves are young and tender, but they persist in the fully-developed leaf without increasing in number. We used to think that these pits were caused by the spines of the old leaves, which pricked the young leaves at times of high wind, but we have now been led to adopt a different explanation. The pits do not actually perforate the leaf-blade; they commonly enter but do not pass through the mesophyll. Holly-trees which are not infested by flies do not show pits on the leaves, but those which are much blistered are also much pitted. Moreover we have seen

the female fly piercing the leaves with her ovipositor. She makes an incision with her pointed ovipositor, then steps backward and applies her tongue to the wound, as if she were extracting sap from the cells. Her movements at this time remind us of the way in which a fowl scratches the ground in search of a worm, and then steps back to examine the loosened soil. Egg-laying is a work of time with the holly-fly, for all the eggs are laid separately, and the female requires a regular supply of food. We have no reason to suppose that the male fly is able to draw sap from the cells of the leaf; it has to be content with what it finds on the leaf. Feeding-holes are made only in young and tender leaves; the ovipositor could not be made to penetrate an old leaf. Sometimes the fly fails to find the hole made by her own ovipositor, and then she makes another. While feeding the female is often visited by the male. When he is on the same leaf he seems to be guided to the spot by the working of the ovipositor; his movements become more alert as soon as he is aware of the presence of the female. Stealthily approaching while the female is absorbed in the act of feeding, he effects a secure embrace, from which he is not easily dislodged. The fertile female now proceeds to lay her eggs. She selects young leaves, but is now careful to pierce the under-side of the midrib, preferring a point near the base of the leaf. The piston-like ovipositor is repeatedly pressed up and down until the central vessels are reached. Then, by a contraction of the abdomen, an egg is passed into the hole. The fly tests the place with her tongue, and when satisfied goes off to another leaf. Thin sections through the place of oviposition show that a vertical shaft ascends from the hole; on reaching the vessels it makes a right-angled bend, and runs for a short distance along the vein; the egg is deposited in the horizontal part of the shaft. That the ovipositor is able to bend at a right angle can be made out by watching live flies. A captive female sometimes lays her egg, not in the midrib, but in the blade of the leaf, and this is, in a young leaf, sufficiently translucent to enable us to follow the action of the ovipositor. The wound made in the midrib is speedily closed by cork-cells.

The egg (fig. 20) is of oval shape, and lies lengthwise in the midrib. One end is blunter than the other, and bears the micropyle; this end is turned towards the opening by

which the egg was passed into the leaf. There are two egg-envelopes, an external chorion, which is yellowish, finely pitted, and prone to adhere to the vessels of the midrib, and a transparent vitelline membrane. The head-end of the embryo is at first adjacent to the micropyle, and therefore points to the mouth of the passage, but before hatching the embryo reverses its position, as if to facilitate the travelling of the larva along the vessels towards the apex of the leaf.

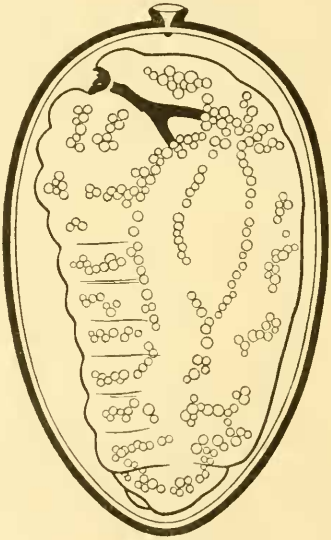

Fig. 20.

Egg with unhatched larva taken from midrib of holly-leaf. (× 165.)

In the fresh-hatched larva segmentation is already complete, and the mouth-parts are well developed. The fat-body, which contains the residue of the fat-globules of the egg, is scanty. The tracheal system is filled with air, but does not as yet open to the exterior. Numerous fine denticles are already developed on the surface of the body. The alimentary canal contains no solid food.

Very little change in the appearance of the larva can be noted so long as it remains in the midrib; the fat-body enlarges, and the fat-globules become more numerous.

As soon as it begins to feed on the mesophyll-cells the calcareous concretions form in the fat-body, and these become conspicuous when the body is examined by transmitted light as large, brightly-refractive objects.

The mode of life of the free larva has been related in an earlier part of the present paper (pp. 259, 260).